ROSES AND THEIR CHROMOSOMES

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INTRODUCTORY

FORTY-FIVE years ago, attracted by the difficulties they presented, I undertook the study of the British wild roses. At first, my efforts were restricted to a consideration, experimentally and otherwise, of their classification, genetics and general biology. As a result, there appeared in 1920 a lengthy illustrated article bearing the title "The Genus *Rosa* its Hybridology and other Genetical Problems". This was published in the *Transactions of the Natural History Society of Northumberland, Durham and Newcastle upon Tyne*, N.S. vol. 5, Part 2, 244–326.

THE STATUS OF BRITISH ROSES

(*a*) *The Import of Defective Pollen*

During the course of my investigations, several remarkable features emerged. Amongst them was the fact that, in the case of all British roses except the Field Rose, *Rosa arvensis*, and the Burnet Rose, *R. spinosissima*, the pollen was characterized by a greater or less amount of imperfect grains.

Now, Dutrochet and Gaertner had demonstrated, quite conclusively, that in most plant hybrids pollen abortion was prevalent. In fact, it became clear that, in many plants, the presence of imperfect pollen could be employed as a test of their hybrid origin. Later, Cole restated the view and emphasized its importance. Accepting these facts, I came to the conclusion that the majority of our wild roses had originated in hybridity. Obviously, such hybridity could not be regarded as of recent occurrence, for putative parents are lacking. It could only be assumed that the original crossing had taken place, long ago, probably in the closing stages of the Ice Age, and that the hybrid constitution had, by some means, persisted since that period. In other words, our roses, for the most part must be regarded as crypthybrids.[1]

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[1] Not appearing to be hybrid, but actually of hybrid origin.

(b) *The Significance of Apomixis*

Manifestly, if much, or all, of the pollen in any particular form is imperfect, then that fact establishes a definite barrier to its reproducing its kind. That circumstance led to a long series of critical experiments in the field which demonstrated amply that, in many of our British species, seeds could develop apomictically, i.e. without pollination and subsequent fertilization. Here, once more, we have a further indication of the hybrid status of such of our wild roses for Ernst (1918) has shown that there is an intimate relation in the way of cause and effect between hybridity and apomixis.

CYTOLOGICAL OBSERVATIONS

Clearly, the various problems called for a new line of attack. It seemed essential that the whole of the available rose species and varieties should be subjected to careful cytological examination. This requirement resulted from Rosenberg's classical work in which he studied the cell behaviour of the hybrid between the two sundews, *Drosera rotundifolia* and *D. longifolia*. That investigation demonstrated that the chromosomes in such hybrids exhibited noteworthy and characteristic peculiarities in behaviour.

Here a digression must be made to supply information necessary for the understanding of such work. Just as is the case with other plants and animals, a rose plant is built up of an enormous number of units we call cells. These cells, in turn, display a definite organization. No matter what its shape is, each cell consists of two easily recognized parts, the cytoplasm and the nucleus, the latter being a more or less spherical body lying within the general cytoplasm. Other structures occur, but they are not pertinent in our present investigation.

The ordinary body cells increase in numbers by a curious method of indirect division called mitosis. When a cell is in a resting condition, the chromatin (the material of which the nucleus is constituted) is so distributed as to form a kind of network. However, in preparation for a division, the chromatin gives rise to a number of bodies known as chromosomes. A chromosome, therefore, is a mass of chromatin, and it should be made clear that the number of such chromosomes in the somatic (or body) cells of any particular plant or animal is constant. Thus a somatic cell from an aspen has 38 chromosomes whilst the number in a similar cell of the common blue butterfly is 46.

Chromosomes obtain their name from the fact that, when they are treated with certain dyes, these dyes are taken up so that the individual chromosomes and their behaviour can be observed much more readily. The importance of this possibility will be appreciated the more when it is stated that the chromosomes carry the genes (or factors) necessary for the development of the characters of an organism. In other words, they play a major role in heredity.

In the division of ordinary body cells, the chromosomes assemble to form what is termed an equatorial plate where their numbers may be counted. There they divide to give rise to 2 sets of equivalent chromosomes, 1 set passing into each of the 2 daughter cells. In this way, the chromosome number characteristic of a species is maintained in the body cells.

In the germ-cell line, however, at a certain division, known popularly as the reduction division, the chromosomes appear on the equatorial plates in pairs, like chromosomes derived from the 2 parents coming together. Hence, when the cell divides, each daughter cell becomes endowed with half the number proper to the species. This process is called meiosis, and results in the gametes or sex-cells likewise possessing a reduced chromosome number equal to one-half the specific number.

My cytological investigations were commenced in 1918, and very early indeed I discovered that the base number of chromosomes in *Rosa* was 7 so that the lowest possible number of chromosomes in a rose species is 14. Such a rose is termed a diploid, i.e.,[1] it possesses twice the base number found in the genus. A British example of such a species is *Rosa arvensis.* More important by far than this was the discovery of many roses with the chromosome complements of 28 and 35. These facts were published on page 277 of the paper mentioned above, and thus provided the first announcement ever made of the existence in the genus *Rosa* of a polyploid series based on the number 7. To quote my exact words "Every rose I have examined appertaining to the Tomentosae, Afzelianae, Eucaninae and Rubiginosae has been endowed with a chromosome number of 35, and is therefore pentaploid whilst the Villosae and Pimpinellifoliae possess 28, and are therefore tetraploid." It is obvious that the species covered by this statement include practically the whole of our British roses, and it proves conclusively that Hurst and others were wrong in assigning to Täckholm the credit for the discovery. The results of my labours were published in April 1920; Täckholm's pronouncement appeared in December 1920.

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[1] Similarly, a rose with 3 sets of chromosomes has 21 in all and is triploid, one with 28, tetraploid, one with 35 pentaploid and so on.

My work began with a study of chromosome behaviour during pollen development in the Caninae or dog roses. It is not difficult to understand that difficulties must occur during meiosis in the case of pentaploids, and numerous irregularities were detected in species with 35 chromosomes. What was not expected was the occurrence of similar phenomena in the triploid Downy Rose, *R. villosa*, and the tetraploid Red-leaved Alpine Rose, *R. rubrifolia.*

Moreover, the anomalies encountered were of the same order as those observed in Rosenberg's sundews. It is, therefore, a fair inference to make that, since that worker was concerned with a recognized hybrid, my material was of a similar constitution. Further, since my plants reproduced apomictically, that circumstance explains the process by which the various forms have maintained themselves during the period which has elapsed since hybridity first brought them into being.

Nevertheless, at least one British tetraploid the 'Burnet Rose', *R. spinosissima,* proved to be quite regular in its meiosis, and produced a high percentage of sound pollen. Moreover, instead of showing an apomictic type of reproduction, it reproduced sexually.

Turning now to the hexaploids, again differences were observable. Some, like *R. nutkana* and *R. moyesii* pass through a normal meiotic phase whilst others, as exemplified by *R. jundzillii* and certain forms of the Briar, *R. micrantha,* behaved like hybrids.

To differentiate these two types of behaviour at meiosis, the term "balanced" was introduced by me to cover tetraploids and hexaploids showing a regular meiosis; on the other hand, tetraploids, pentaploids and hexaploids, in which the course of events at meiosis was abnormal, were described as "unbalanced".

In the unbalanced species and varieties, on the male side, the equatorial plate at the meiotic stage reveals an assemblage of 7 pairs of spaced chromosomes in the centre surrounded by an array of single chromosomes more or less regularly disposed. In the ensuing division, far-reaching disturbances arise which lead ultimately to the formation of defective pollen grains. Still, on rare occasions, functional pollen grains do develop. These invariably possess a chromosome complement of 7, as do the resulting generative nuclei or gametes.

In preparation for the production of the egg-cell, meiosis again pursues an exceptional course which departs profoundly in pattern form that in pollen formation; it ends in female gametes carrying 21, 28 or 35 chromosomes, the difference depending upon whether or not the parent plants were tetraploid, pentaploid or hexaploid respectively.

That gametes on the male side with 7 chromosomes and those with 28 from a female parent can fuse in fertilisation is proved convincingly by a pentaploid in my possession. This originated in a cross between the 'Hairy Dog Rose', *R. dumetorum*, acting as female parent and a tetraploid 'Downy Rose', *R. villosa*, playing the role of male. From it I have raised quite a number of apomictic offspring in a second hybrid generation. These show no evidence of Mendelian segregation. The importance of this experiment is great, and lies in the proof it affords that, even today, new rose forms can arise as hybrids and perpetuate themselves by apomixis.

POLYPLOIDY IN THE GENUS

Throughout the above remarks, the terms tetraploid and pentaploid have been used freely. It is necessary now to consider the word "polyploid". When in a given plant or animal genus the various members possess chromosome complements which are multiples of a common base number, these complements are said to form a polyploid series. Thus in *Rosa* we have diploids, triploids, tetraploids, hexaploids and octoploids forming a polyploid series based on the number 7. Each individual member of such a series is regarded as "orthoploid" whilst a species carrying a chromosome number not an exact multiple of the base is termed "aneuploid" or "anorthoploid". How do polyploid series arise? becomes the next question we must ask ourselves. Taking due cognizance of the meiotic and the other phenomena observed in our triploids, pentaploids and unbalanced tetraploids and hexaploids, we have been forced to conclude that they, for the most part, have originated in acts of hybridity. This observation harmonizes with the usual theories put forward to account for the development of polyploid series in plant genera. It fails to account for the higher balanced members of a series.

It is plain that, since 7 is the base number in *Rosa* and diploid forms still exist, some must be of early origin, and may have participated in the movements which were responsible for the evolution of polyploids.

The simple crossing of two diploids would yield a hybrid, which, if its chromosomes paired regularly at meiosis, would give rise to a series of plants displaying a wide range of variation, due to Mendelian segregation and recombination. Upon such an array, selection, natural or artificial, could work so as to establish new diploid species or varieties. If the chromosomes behaved irregularly at that stage, then sterility, total or partial, would arise and provide a block to further progress. Should, however, a duplication of the chromosome complement take place, by accident or otherwise, in these sterile hybrids then a new fertile tetraploid would be generated.

That such an event can happen whereby a higher polyploid can come into being is readily demonstrated. *R. wilsonii*, a rose found on the Menai Strait, is a hybrid between *R. spinosissima* and *R. sherardi*, the latter being the pollen parent. Theoretically, therefore, its chromosome complement should be 14+7, since *R. spinosissima* is a fertile, sexual tetraploid, and functional male gametes of *R. sherardi* have 7 chromosomes. Contrary to expectation, however, when its cytology was examined, *R. wilsonii* turned out to possess 42 chromosomes and to be hexaploid. In other words, by some means, chromosome doubling had occurred. Quite unexpectedly, too, *R. wilsonii* was found to be balanced and fertile in spite of the fact that the reciprocal hybrid is unbalanced and sterile. Thus, by the fertilization of an egg-cell with 14 chromosomes by a gamete resulting from a pollen grain with 7, followed by chromosome duplication, a fertile hexaploid has arisen.

Such happenings as those just discussed have, no doubt, been responsible for the development of polyploid series in *Rosa*, *Salix*, *Chrysanthemum* and other plant genera.

It should be noted that they must have taken place on numerous occasions in *Rosa* for in its various sections, the polyploid series are quite independent. Consider, for example, the Section Cinnamomeae; beginning with the diploid *R. cinnamomea* there follow the tetraploid *R. pendulina*, the hexaploid *R. nutkana* and the octoploid *R. acicularis*. Again, in the Carolinae we have the diploid *R. nitida* and the tetraploid *R. lucida* and in the Spinosissimae the diploid *R. hugonis* and the tetraploid *R. spinosissima*.

A NEW METHOD OF POLYPLOID SERIES BUILDING

Much more curious and interesting is a method of polyploid origination in certain hybrids of *Rosa spinosissima*. This depends, it is true, on hybridity, but is so novel in its mode of action that it deserves special treatment.

In general, the 'Burnet Rose' hybridizes freely with members of the sections Eucaninae, Villosae and Rubiginosae, and thereby produces almost sterile pentaploid and hexaploid first generation hybrids. Despite their sterility, such hybrids do yield, on rare occasions, a few good seeds. If these are planted they germinate well, and give rise to many normal plants with a few dwarf forms. Amongst the seedlings, orthoploid plants are secured possessing chromosome complements of 14, 28, 35 and 42. In a very striking manner, in one single experiment, a new polyploid series has been brought into being by a very novel mechanism. In addition to these polyploids, there were obtained aneuploid forms with the chromosome numbers 24, 32 and so on.

These, occurrences were not the only remarkable results of this experimental work. Notwithstanding the almost total sterility of the first hybrid generation, the plants furnished with 28 chromosomes, which are in the majority, are fertile and balanced in their tetraploidy. In appearance, they approximate more closely to *R. spinosissima*, but show signs of the other parent in flower colour, leaf shape and vestiture, etc. Such anomalous second generation hybrids were reared from the crosses *R. sherardi* × *R. spinosissima*, *R. coriifolia* (*caesia*) × *R. spinosissima* and *R. rubiginosa* × *R. spinosissima*.

HURST'S VIEWS AND RESULTS

My old friend Dr. C. C. Hurst held very different opinions about the development of polyploids in *Rosa* from those enunciated above. He postulated that all were derived from a Boreal decaploid species. This he pictured as possessing 70 chromosomes built up of 2 lots of 5 differential septets or sets of 7. He urged that, for various reasons and under many circumstances, whole sets of 7 had been lost successively to yield rose species in the cytological position we now find them. Such a process, if it did take place, would undoubtedly explain the polyploid chains now exhibited by *Rosa*.

Much as one wished to accept Hurst's views, cytological evidence, in the main, failed to support him. As a result, his theory of differential septets has been abandoned tacitly.

Still, one cannot but admire the ardour with which he pursued his chromosome researches, and their great value in formulating a reasonable understanding of the genus.

Outstanding in his contributions to our knowledge was the determination of the chromosome numbers and behaviour in nearly a thousand species and varieties. On this side of his work he tackled not only the relatively easy process of pollen formation, but also the much more difficult task of following the development of the egg-cell.

Although during the course of my own researches many new chromosome numbers were made available, there seems little to gain by repeating them here. Not only did Hurst cover practically the same ground in his paper in the 1929 *Rose Annual*, but in addition he supplied valuable information about the cytology of many cultivated forms. He demonstrated, for instance, that many of the climbers like the 'Crimson Rambler' were diploids as were also the bulk of the tea roses, with a curious exception in the case of 'Lady Hillingdon' which was triploid. Similarly, he showed for the first time that the hybrid perpetuals were tetraploid. These and other significant facts are set out in his 1929 publication. To that paper recourse should be made for such information.

IS FURTHER PROGRESS AMONGST CULTIVATED ROSES POSSIBLE?

As was explained above, the chromosomes play a major part in the heredity of an organism. Therefore, if it is desired to obtain new forms from old ones, in some way or other the chromosomes in the latter must be influenced, either by changes involving whole complements or in respect to the genes individual chromosomes carry. In *Rosa* many of the enormous strides that have been made in the way of producing new varieties have depended upon the ease with which the different species may be crossed, coupled with the possibility of vegetative propagation.

In the past breeders have, by a sort of mass hybridization, combined the 'Chinese Rose', *R. chinensis*, with the 'Provins Rose', *R. gallica*, the 'Cabbage Rose', *R. centifolia*, and the 'Tea Rose', *R. odorata*, to form the hydrid perpetuals and teas, thereby creating new varieties displaying the desirable qualities of several species. This suggests that planned breeding with a knowledge of the chromosome number of the species involved, may give rise to untold novelties in the future. Nowadays, such plans need not be confined to experiments with old-fashioned species, for many desirable roses like *R. moyesii* simply call for inclusion in the chain. Like other species, it has much to offer in extending the list of the marvellous forms now in culture.

However, it must be remembered that many estimable varieties owe their origin to bud mutations also perpetuated vegetatively. Formerly, mutations were merely matters of chance. Today, by means of X-rays or rays emanating from radioactive substances, mutations can be produced at will as has been shown in tobaccos, cotton and various cereals. Some of these mutations are valuable so that if this technique is applied to roses some really worthy forms may be obtained.

Again, it has been discovered that chromosomes may be affected in another way. The chemical, colchicine, derived from the corms of the Autumn Crocus, *Colchicum autumnale*, has the power of suspending mitoses, and thereby bringing about the doubling of chromosome numbers. It may be applied to seeds and seedlings, and to the growing points of twigs and buds, either in aqueous solution or in lanolin. Amongst other plants, clovers, tobaccos, snapdragons and petunias have all yielded to colchicine treatment, and given rise to improved varieties.

Lastly, it may be applied successfully to first generation sterile hybrids where it not only doubles the chromosome numbers, but brings about fertility. Thus the unfortunate fact that many desirable roses like 'Mermaid' and 'Frensham' are sterile need no longer daunt rose-breeders. Almost certainly, the application of colchicine to growing points would give rise to doubled chromosome numbers and to fertility in the branches affected. In this manner further crossings with these hybrids would certainly become possible.

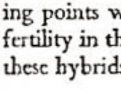

Fig. 1.
Balanced tetraploid,
R. spinosissima.

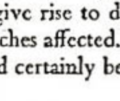

Fig. 2.
Unbalanced tetraploid, *R. villosa.*

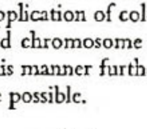

Fig. 3.
Unbalanced pentaploid, *R. canina.*

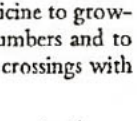

Fig. 4.
Unbalanced hexaploid, *R. jundzillii.*